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RESEARCH ARTICLE

Social Facilitation of Exploratory Foraging Behavior in Capuchin Monkeys (*Cebus apella*)

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Much of the research on animal social learning focuses on complex cognitive functions such as imitation and emulation. When compelling evidence for such processes is not forthcoming, simpler processes are often assumed but rarely directly tested for. In this study we address the phenomenon of social facilitation, whereby the presence of a feeding conspecific is hypothesized to affect the motivation and behavior of the subject, elevating the likelihood of exploration and discovery in relation to the task at hand. Using a novel foraging task, sufficiently challenging that only just over half the subjects successfully gained food from it, we compared the performance of capuchin monkeys working either alone, or in a ''social'' condition where an actively feeding conspecific was in an adjacent chamber. Although similar numbers of subjects in these conditions were eventually successful during the 20 trials presented, the latency to successful solution of the task was over three times faster for monkeys in the social condition. The minority of monkeys that failed to learn (9/23) were then exposed to a proficient model. Only those older than 5 years provided evidence of learning from this. Accordingly, we obtained evidence for the social facilitation the study was designed to test for, and limited supplementary evidence for social learning in the older individuals who had not learned individually. These results are discussed in relation to other recent evidence for social learning in monkeys. Am. J. Primatol. 71:419–426, 2009. © 2009 Wiley-Liss, Inc.

Key words: individual learning; innovation; trial-and-error learning; social facilitation; *Cebus apella*

INTRODUCTION

Historically, the study of social learning and culture in animals has concerned itself with cognitively complex mechanisms of social learning, with particular emphasis on imitation. This has been particularly true in primatology [Tomasello & Call, 1997; Whiten, 2000]. However, recent advances in the study of cultural diffusion and behavioral innovation in animals are beginning to shed light on a more basic aspect of cultural propagation, that of individual differences in motivational states [Huber et al., 2001; Kendal et al., 2005; Laland & Reader, 1999; but see Reader & Laland, 2001 for review]. Zajonc [1965] suggested that an individual's motivational state might be inhibited by the ''mere presence'' of another individual. Social presence alone has been shown to have an effect on the behavior of other individuals, but not only in inhibiting behaviors; in some cases, the mere presence of a conspecific can increase an individual's motivational state and therefore also enhance its interest in engaging in a behavior [Addessi & Visalberghi, 2001; Galloway et al., 2005; Thorpe, 1963; Voelkl et al., 2006]. This is commonly referred to as *social facilitation*, but is also referred to as *social enhancement* as the motivational state of an individual is accentuated by another (be it an increase or decrease in motivation) [Clayton, 1978]. This phenomenon is considered to be an important social mechanism for group living species, including humans, because of its influence on group cohesion, behavioral coordination, foraging efficiency, and predator avoidance [Boinski & Garber, 2000; Caro & Hauser, 1992; Chalmeau & Gallo, 1993; Coussi-Korbel & Fragaszy, 1995; Fragaszy et al., 1994].

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Ueno [2005] found that infant and juvenile Japanese macaques (*Macaca fuscata*) engage in synchronous feeding behavior when other group members are feeding within 1 m of them. The act of synchronous behavior is thought to provide ideal observational learning opportunities for acquiring information about palatability, preference and processing of novel foods. This may be important for Japanese macaques, who exhibit group-specific traditions such as wheat or potato washing, and stone handling [Huffman, 1996; Huffman and Quiatt, 1986; Kawai, 1965], as well as for a number of other species that increase and coordinate feeding in the presence of other feeding conspecifics [fish, Pitcher & Parrish, 1993; capuchin monkeys, Galloway et al., 2005; chickens, Tolman, 1964; dogs, James, 1953; pigs, Hsia & Wood-Gush, 1984; and hyenas, Yoerg, 1991].

With regards to cultural learning, however, the effects of social facilitation are largely ignored in the primate literature in favor of a more distinctive and cognitively complex form of social learning: imitation. It has been argued that, along with language and the ability to teach, the ability to imitate others is at the heart of human cultural complexity. Evidence for imitation and complex culture in apes has strengthened this view that imitation is the ‘‘holy grail'' of cultural learning [Matheson & Fragaszy, 1998; van Schaik, 2003; Whiten et al., 1999, 2005]. Although the significance of imitation cannot be doubted, it remains unclear what alternate forms of social learning contribute to, or possibly even inhibit, the development of group-specific behaviors, particularly cultural variation in populations of monkeys. Japanese macaques and white-faced capuchins (*Cebus capucinus*) exhibit culturally distinct behaviors across wild populations [Leca et al., 2007; Nahallage and Huffman, 2007], yet experimental evidence has suggested that they, and other monkey species, rarely imitate conspecifics the way apes and humans may do [Adams-Curtis & Fragaszy, 1995; Fragaszy & Visalberghi, 2004; Visalberghi & Fragaszy, 2002]. Although more recent examples of imitation in marmosets and capuchins are emerging, these observations are much less frequent than those in apes and suggest less complexity in copying [Bugnyar & Huber, 1997; Dindo et al., 2008; Fredman & Whiten, 2008; Voelkl & Huber, 2007]. For this reason, studying social learning in monkeys should take account of the ‘‘collective outcome of interacting physical, social, and individual factors'' [Fragaszy & Visalberghi, 2004, p. 24].

In addition to understanding the kinds of copying that allow certain behaviors to spread throughout a group (e.g. imitation, emulation, and object movement re-enactment), we must also begin to explore the social contexts that support opportunities in which social learning can occur. Social facilitation remains noticeably under-represented in the literature despite its strong potential for supporting the transmission of behavior through group cohesion (i.e. increasing opportunities for learning), and behavioral coordination (i.e. synchrony that leads to matching or copying of behavioral activities). King [1994] suggested that synchrony of feeding will result in individuals consuming the same food because of the close distribution of food patches. Similarly, Galef [1993] argued that if social facilitation influences an individual's motivation to consume familiar food in the presence of another feeding conspecific, then this presence will be even more significant to whether or not an individual is willing to accept a novel food. Although this may be in part owing to a reduction in neophobia to the novel food item, it may also be a result of an increase in motivation to eat [Ferrari et al., 2005; Harlow & Yudin, 1933; Visalberghi & Addessi, 2000].

This study of brown capuchin monkeys (*C. apella*) aimed to study differences in individual motivation for learning a new foraging task in the presence or absence of a feeding conspecific. Dindo and de Waal [2007] found that capuchin monkeys increase their collection and consumption of a low-valued food when in the presence of a feeding conspecific, regardless of what quality of food the conspecific is eating. Furthermore, when food is present, but the conspecific cannot access or eat the food, capuchins will consume their food at speeds similar to when they are alone, speeds that are significantly lower when compared with the joint feeding condition. Other studies in capuchin monkeys [Addessi & Visalberghi, 2001; Galloway et al., 2005] have found similar effects of social facilitation of food consumption, suggesting that capuchins are highly sensitive to the presence of feeding conspecifics, and that their own motivational state may be significantly enhanced by the mere presence of feeding individuals.

Given the strong evidence for social facilitation in capuchins of behaviors already within their repertoire, we were interested to see whether this enhancement of their motivational state would translate to an increased motivation for exploratory behavior and potential discovery of a new foraging technique. To test this, we designed an apparatus that could be manually manipulated to release visible food from behind a barrier. This task required several directional pushes, and therefore required an individual to spend time prodding the apparatus. We presented subjects with this apparatus either (1) in the absence of a conspecific, or (2) in the presence of a feeding conspecific who had food, but did not have to work for the food. We predicted that subjects would increase their exploratory foraging behavior and therefore learn to extract food from the apparatus faster in the social feeding condition than in the alone condition.

METHODS

Subjects and Housing

The subjects included 24 brown capuchin monkeys housed at the Yerkes National Primate Center in Atlanta, GA. The capuchins ranged in age from 2–40 years old (median 7 years) and belonged to two separate groups of 15 (A) and 15 (B) monkeys (Table I). The indoor and outdoor home enclosures for each group measured 25 m^2 (A) and 31 m^2 (B) in total. Subjects had access to lab chow and water ad libitum and were never food or water deprived. The experimental conditions, foods presented, and subjects included in this study were all approved by the Institutional Animal Care and Use Committee (IACUC) of Emory University before the start of the study, which was conducted from May 21 to June 25, 2007.

Apparatus

The apparatus used in this study was made of clear lexan and measured 28 × 28 × 28 cm. The front panel (28 × 28 cm) had a 13 cm horizontal incision located 13 cm above a small food cup. Protruding from the incision was a clear lexan wheel that measured 18 cm in diameter and had a 2 cm diameter hole (at the 6 o'clock position for the monkey's perspective) in which food rewards were placed (Fig. 1a). Below the hole was a support panel; food would not fall through this until the wheel was rotated to where the hole lined up with a chute (at the 12 o'clock position), which released the food into the small food cup (Fig. 1b). Brightly colored Trix® cereal (General Mills, Minneapolis, MN) was used as a food reward so that it was clearly visible through the front panel. The wheel could be rotated by pushing left or right on the protruding piece on the front panel. The back of the box was open, so that the experimenter could bait the hole with food rewards and rotate the wheel back to the ''start'' position. The start position is defined by having food presented where the subject could see the food baited in the hole at the 6 o'clock position (Fig. 1a).

Procedure

Test subjects were separated from their group by a familiar and routine procedure, which lasted no more than 30 minutes. Tests were conducted indoors in front of each respective group's home enclosure in a test chamber measuring 144 × 60 × 60 cm. A mesh partition was inserted into the test chamber to create two compartments of 72 × 60 × 60 cm (Fig. 2). All subjects were tested in the left compartment. The back of the test chamber was opaque to prevent group members from viewing the test condition and apparatus. The front of the test chamber was made of clear lexan paneling with 2.5 cm armholes through

TABLE I. Individual Results. Results by Subject and Experimental Condition, Along With Each Subject's Success as a Learner, or Non-learner

Subject	Sex	Age	Condition		First success (1st trial)	Total test (start to finish)	Last 19 trials (1–20 trials)
Georgia (GE)	F	22	Alone	Learner	15	277	262
Winnie (WN)	F	23	Alone	Learner	61	530	469
Bias (BI)	F	20	Alone	Learner	98	638	540
Lucas (LC)	M	7	Alone	Learner	513	731	218
Ike (IK)	M	33	Alone	Learner	502	791	289
Lancey (LA)	F	5	Alone	Learner	655	959	304
Snarf (SN)	M	3	Alone	Learner	769	1100	331
Star (ST)	F	35	Social	Learner	19	201	182
Benny (BE)	M	3	Social	Learner	30	236	206
Nancy (NN)	F	22	Social	Learner	79	284	205
Nate (NT)	M	3	Social	Learner	24	387	363
Mason (MS)	M	9	Social	Learner	226	539	313
Sammie (SM)	F	11	Social	Learner	74	633	559
Nicole (NI)	F	7	Social	Learner	249	690	441
Wilma (WL)	F	9	Social	Non-Learner	62	407	345
Goya (GY)	F	14	Alone	Non-Learner	45	281	236
Gretal (GR)	F	3	Social	Non-Learner	x	x	x
Scarlett (SL)	F	2	Social	Non-Learner	x	x	x
Luther (LH)	M	2	Social	Non-Learner	x	x	x
Lark (LR)	F	5	Alone	Non-Learner	x	x	x
Winter (WT)	F	3	Alone	Non-Learner	x	x	x
Wookie (WO)	M	3	Alone	Non-Learner	x	x	x
Mango (MG)	F	40	Alone	Non-Learner	x	x	x

The first success, total test, and last 19 trials are all shown in seconds, with the non-learners' results after the observation condition. Failures are marked by an 'x'.

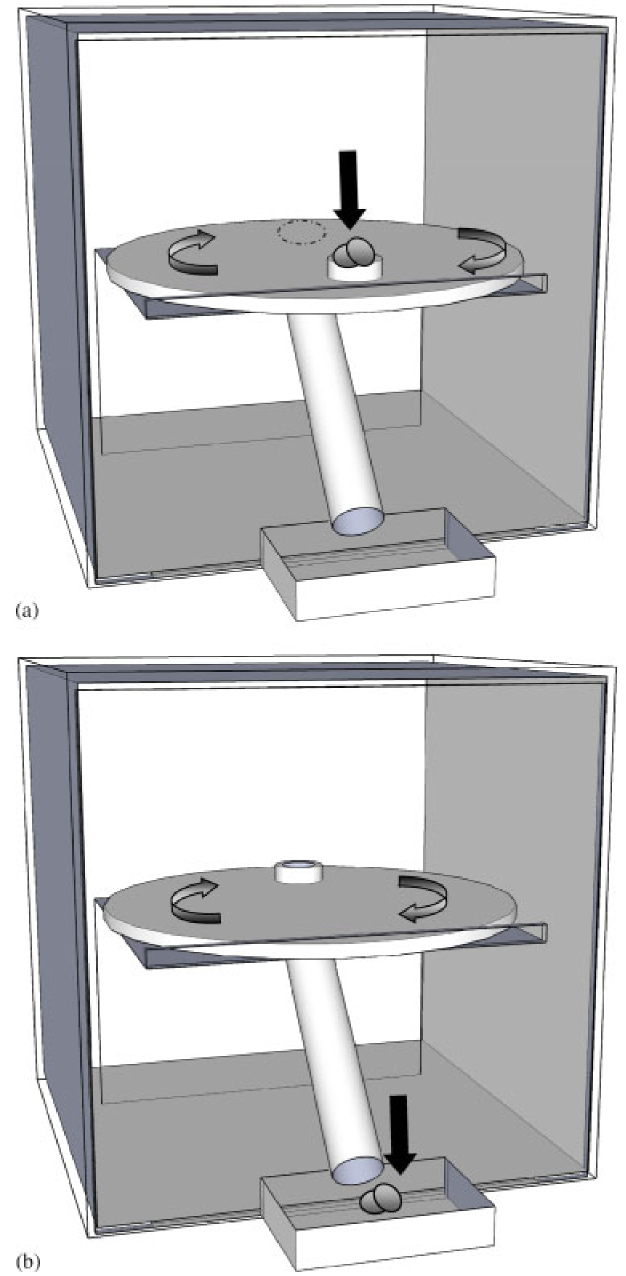

Fig. 1. **a** and **b**. The figures (a and b) show the apparatus as it was presented to the subjects. A small surface of the wheel extended out through the front panel, allowing it to be rotated when pushed either left or right. The black arrow in Fig. 1a shows the food behind the clear front panel in the 6 o'clock start position. The side arrows indicate that the wheel can be rotated to line up with the chute at the 12 o'clock position. Once the food is rotated to the 12 o'clock position, it lines up with a hole and falls down the chute into the presentation cup (as indicated by the black arrow in Fig. 1b).

which the monkeys could manipulate the apparatus and collect food. All subjects were well habituated to being in the test chamber for testing, both alone as well as with another test partner. Therefore, any potential stress from separation was considered negligible.

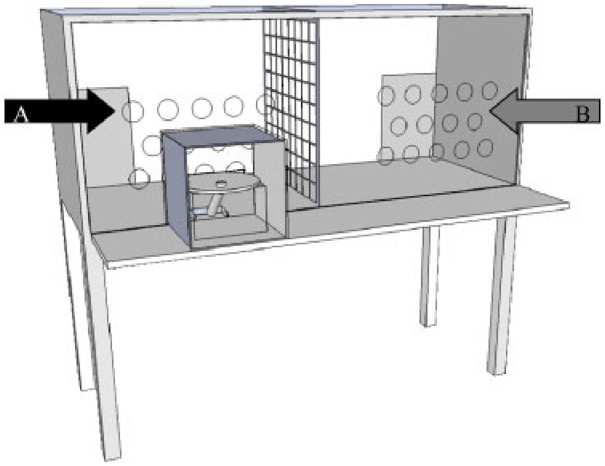

Fig. 2. The test chamber is shown here, divided into two sections by a mesh partition. In both the ''alone'' and ''social'' conditions, the subject was presented with the apparatus in section A (black arrow). In the ''alone'' condition, section B (gray arrow) remained empty, whereas in the ''social'' condition, a feeding monkey was in section B.

Alone and Social Conditions

Twelve subjects from each group were randomly assigned to either the *alone* or *social* condition, so that each condition had 12 subjects, with 6 subjects from each group. A weather disruption prematurely ended one test in the social condition, thus this subject's data were not included here and overall subject numbers were reduced to 23.

In the alone condition, one test subject was alone on the left side of the test chamber, whereas the right side remained empty. The experimenter presented the subject with the apparatus by placing it on a tray in front of the armholes of the test chamber. The experimenter immediately lifted a piece of cereal above the apparatus until the subject looked at the food, and then placed the cereal into the holder on the wheel, which was positioned at 6 o'clock relative to the subject. The subject then had 15 min in which to retrieve food from the apparatus by turning the wheel in either direction. If the subject was successful at pushing the wheel 180° (to the 12 o'clock position), the hole lined up with a chute and food fell into the food cup for collection. The experimenter would then rotate the wheel back to the start position (6 o'clock), returning the hole to the front of box with a new piece of cereal in view for the subject. This constituted the beginning of the next trial and the test ended after 20 trials (20 food retrievals). If the subject was unable to rotate the wheel and collect food, the experimenter continued to bait the hole with food every 1 min for 5 min (i.e. a total of five pieces in the hole). After that, and if necessary, the experimenter picked up one of the five pieces, showed it to the subject, and placed it back onto the pile every minute for a further 10 min, to show that food was still being presented for collection. All tests ended after 20 trials or after 15 min without success.

The same protocol that was used in the alone condition was applied to the social condition, but a conspecific monkey was present in the right compartment of the test chamber. The monkey on the right side of the test chamber was presented with a cup of Trix® cereal and peanut butter. Peanut butter was used because the monkeys consumed this food slower than the cereal, thus ensuring that the partner would be eating for the majority of the 15 min test and not soliciting food from the test subject. The conspecific monkey was a monkey from the alone condition who had successfully extracted food. That individual was not able to reach the apparatus through the mesh partition or assist in moving the wheel in any way. No monkeys were presented with the opportunity to watch a conspecific retrieve food before testing in the Alone or Social conditions. All subjects were naïve to the apparatus before the test.

Non-learner Post-testing

In the event that an individual was unable to learn how to manipulate the apparatus for food, the test ended after 15 min. Within a month of completing each of the subjects' tests, the non-learners were tested for a second time, but this time after having the opportunity to watch a subject from their social group that had been successful at manipulating the apparatus. Non-learners were allowed into the left side of the test chamber while a group member demonstrated 40 trials in his or her presence. After the demonstrations, the demonstrator moved over to the right side of the test chamber and was given Trix® cereal and peanut butter as was done in the social condition. The non-learner subject then had 15 min, or until 20 trials were completed, to interact with the apparatus.

Data Collection and Analysis

All tests were videotaped using a Canon mini-DV recorder (Canon Elura 90, Tokyo, Japan). The experimenter placed the first piece of cereal into the holder and said, ''start of the test''. This marked the start of the test and was considered the 0 sec timestamp for coding that test.

Tapes were coded by the first author for the time in seconds between the 0 sec mark and successful food collection (i.e. when food was collected from the cup) by recording the time in seconds for each trial. As the latencies were continuous data points, we first tested for normal distribution and then used parametric statistics for analysis. Independent sample *t*-tests were used to compare means and reported with two-tailed *P*-values.

RESULTS

The overall latency (Fig. 3: ''Total Test'') of each test was measured as the number of seconds it took from the start (presentation of the apparatus at 0 sec) to the end of the test (completion of 20 trials). In the event that a subject was unable to manipulate the device for food, a latency of 900 sec was recorded, as the tests were 900 sec in duration.

Comparing the overall latencies of each condition, we found no significant difference between the alone and social subjects' performances ($t(21) = 1.26$, $P = 0.220$, $N_A = 12$, $N_S = 11$). However, this analysis lumps social learners and non-learners. We next conducted separate tests for learners and non-learners. In the alone condition, 7 out of 12 subjects were considered ''learners'' because they discovered how to rotate the wheel and successfully collected food for all 20 trials. In the social condition, 7 out of 11 subjects were considered ''learners'' by the same criterion. In total, nine subjects were thus non-learners (Table I).

Learners

Clearly, learners were no more common in the social than the alone condition. However, when we compared the learners from the alone condition ($N_A = 7$) with the learners from the social condition ($N_S = 7$), we found a significant difference in the speed of learning between the two conditions, with subjects in the social condition reaching the first successful trial over three times faster on average than those in the alone condition ($t(12) = 2.23$, $P = 0.046$). Subjects in the alone condition had an average latency of 373 sec (SD 309) to the first successful trial, whereas subjects in the social condition had an average latency of only 100 sec (SD 97) to the first successful trial.

Additionally, the overall completion of the tests (start to finish) was significantly faster in the social condition than in the alone condition ($t(12) = 2.31$,

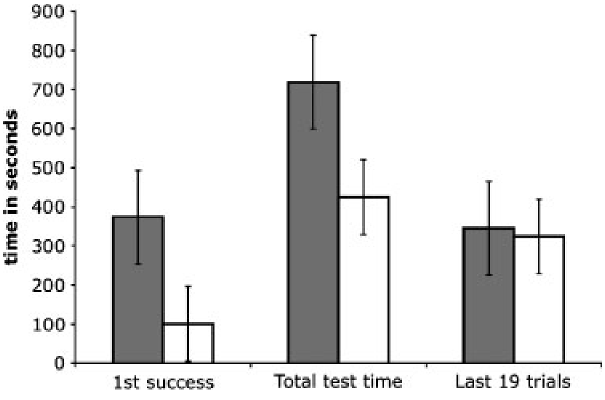

Fig. 3. The average latencies in seconds for (1) first successful food retrieval, (2) total test time, and (3) latency between trials are presented here in gray for the ''alone'' condition, and white for the ''social'' condition along with standard error bars.

$P = 0.040$). Alone subjects averaged 718 sec (SD 273) from start to finish, whereas social subjects had an average speed of 424 sec (SD 197) from start to finish. However, subjects in the social condition did not subsequently perform the task any faster or more efficiently, as is indicated by the similar latencies in completing the last 19 trials (Table I: ''Last 19 trials''). Subjects in the alone condition spent an average of 345 sec (SD 117) manipulating the apparatus for food, and subjects in the social condition spent an average of 324 sec (SD 141).

Non-learners

It was possible to determine if a subject was observing the demonstrator by the eye gaze and body position of the individual, and in most cases, the subject and demonstrator were in physical contact during an observation. All of the nine non-learners watched at least 50% of the 40 demonstrations.

Of those who were deemed non-learners, only three were over 5 years old (Table I). Two were alone subjects, and a third was a social subject. The first, a 14-year-old female, was the lowest ranking member of her social group. The second, a 9-year-old female, was moderately ranked within her group and was generally considered to be a good test subject. The third was a 40-year-old female, who was mildly arthritic. In their tests, after watching a proficient demonstrator, the first two of these monkeys had latencies of 62 and 45 sec, respectively for their first successful trial (c.f. the mean of 100 sec for social subjects that were successful in the original tests), and overall testing latencies of 407 and 281 sec from start to finish. The third adult non-learner touched the wheel repeatedly, but did not move it and collect food even after having observed a demonstration.

Four of the non-learners were juvenile females between the ages of 2 and 5-years old, and two more were juvenile males, aged 2 and 3. None of these juvenile non-learners gained food despite touching and moving the wheel throughout the test sessions.

DISCUSSION

Our results show that capuchin monkeys who were in the presence of a feeding conspecific were successful in a novel foraging task over three times faster than monkeys who were alone with the apparatus. The results were significant for both the first successful food collection and for the overall time it took to complete the test (Table I: ''Total Test''), suggesting that the capuchins' motivation to explore the foraging apparatus was intensified by the presence and behavior of a familiar, feeding conspecific. However, the actual time it took to perform each trial (''Last 19 Trials''), did not differ much at all, suggesting that the monkeys were not faster or more efficient in their performance. Previous social learning experiments have suggested social facilitation as a likely mechanism at work when capuchin monkeys acquire behaviors after observing a conspecific. They suggest that an increased motivation may be responsible for the subject replicating the same results a conspecific model demonstrated. More recent studies have shown that capuchins and other monkeys are capable of more complex copying than previously thought [Dindo et al., 2008; Fredman & Whiten, 2008; Voelkl & Huber, 2007] and direct testing of social facilitation as a specific process has been lacking. Social facilitation may provide the necessary change in motivational state that then leads to an increased willingness to watch others and engage in the same behavior. As Fragaszy and Visalberghi [2004, p 24] have noted, social learning in monkeys is ''always the collective outcome…of richly interconnected processes,'' in which social facilitation may well play a significant role in the learning experience.

Aside from social learning mechanisms, another interacting element is the individual's life history, including age, sex, social status, and physical abilities. Of the nine non-learners, the six juveniles under the age of 5 years were unable to acquire the foraging technique even after watching a demonstrator performing the task. Juveniles are often assumed to be the most likely innovators of novel behaviors, as well as those for whom social learning is likely to be most important [Kendal et al., 2005; Laland & Reader, 1999; Reader & Laland, 2001], but in the context of this study there was no evidence of this. Matsuzawa's theory of learning by ''master apprenticeship'' [Matsuzawa et al., 2001] may offer one possible explanation here, insofar as it may require a much longer period of observation before young individuals are able to acquire the skills necessary to adopt the behavior in question. Another explanation could be that some of the juveniles lacked the coordination and/or dexterity to carry out the task based on their age and sex.

The remaining three non-learners were all adult females. In the case of the oldest, 40-year-old monkey, her motivation to manipulate the device was evident, but her age and dexterity were potential limiting factors in her inability to fully rotate the wheel. It is however safe to say that her age and dexterity were potential limiting factors in her inability to perform the task. The second non-learner was a moderately ranked female in the social condition. The group member in the adjacent section of the test chamber was her higher-ranking mother. It has been reported that low-status monkeys will intentionally inhibit their behavior in the presence of higher-ranking individuals [Drea & Wallen, 1999]. This is a potential explanation for her initial lack of response to the test in the social condition, but not in the social learning condition. However, our study was not designed to take personal relationships into account. Finally, the third non-learner was the lowest-ranking monkey in her group, and although she was tested in the alone condition, she was shy and scarcely motivated to work on the apparatus in the test condition. After the non-learners were presented with the opportunity to watch another group member turn the wheel for food, the two successful adult females completed their first rotation of the wheel and collected food at 62 and 45 sec, respectively. These latencies are within the range seen in the ''social'' condition and are well below the 100 sec average for that condition, suggesting limited supplementary evidence for social learning.

The findings of this study address an area of social learning research in monkeys that has previously been neglected. When we chose to focus on the social influence of feeding conspecifics (as opposed to non-feeding ones), we were aware that previous studies with capuchins (*C. apella*), as well as common marmosets (*Callithrix jacchus*) have found that latencies of food consumption and acceptance of novel foods increase in the presence of other feeding conspecifics [Addessi & Visalberghi, 2001; Dindo & de Waal, 2007; Voelkl et al., 2006]. Ferrari et al. [2005] found that merely hearing the sound of other macaques eating activated motor programs related to eating, suggesting marked sensitivity in monkeys to the activities of others. The subjects of this study, capuchin monkeys, are extremely active individuals who engage in social interactions throughout their days. For these reasons, we believed that a social *feeding* condition would provide an ecologically sound background for investigating a potential motivating force for exploratory foraging in these monkeys. However, this study would have benefited from a control condition in which non-feeding monkeys were ''merely present'' but it was not considered ethical to present a non-feeding partner subject with nothing to do other than watch the subject actively collect food for up to 15 min. Future research should tease apart the effects of foraging versus non-foraging social facilitation effects, using ethically acceptable designs.

We focused on social facilitation specifically here because we believe that negative reports for imitation in monkeys often attributed social facilitation as the underlying mechanism by default, as opposed to any direct experimental demonstration. Voelkl and Huber [2000] found that mere presence had an effect on exploratory behavior in marmosets, facilitating discovery of a method for opening a film canister without the aid of demonstrations. Voelkl and Huber later conducted a more controlled experiment in which they found these monkeys were able to imitate the movements they observed [Voelkl & Huber, 2007]. We do not argue that the imitative abilities of monkeys are the same as those of the great apes or human children, however, social facilitation can speed the process of individual exploration and discovery. In fully social contexts it is also likely to further support group cohesion, and thereby increase opportunities for observational learning and synchronization of behavior between groupmates [Cambefort, 1981].

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